

# Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality

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**Biodiversity encompasses multiple attributes such as the richness and abundance of species (taxonomic diversity), the presence of different evolutionary lineages (phylogenetic diversity), and the variety of growth forms and resource use strategies (functional diversity). These biodiversity attributes do not necessarily relate to each other and may have contrasting effects on ecosystem functioning. However, how they simultaneously influence the provision of multiple ecosystem functions related to carbon, nitrogen, and phosphorus cycling (multifunctionality) remains unknown. We evaluated the effects of the taxonomic, phylogenetic, and functional attributes of dominant (mass ratio effects) and subordinate (richness effect) plant species on the multifunctionality of 123 drylands from six continents. Our results highlight the importance of the phylogenetic and functional attributes of subordinate species as key drivers of multifunctionality. In addition to a higher taxonomic richness, we found that simultaneously increasing the richness of early diverging lineages and the functional redundancy between species increased multifunctionality. In contrast, the richness of most recent evolutionary lineages and the functional and phylogenetic attributes of dominant plant species (mass ratio effects) were weakly correlated with multifunctionality. However, they were important drivers of individual nutrient cycles. By identifying which biodiversity attributes contribute the most to multifunctionality, our results can guide restoration efforts aiming to maximize either multifunctionality or particular nutrient cycles, a critical step to combat dryland desertification worldwide.**

functional diversity | mass-ratio hypothesis | nutrient cycling | phylogenetic diversity | taxonomic diversity

Understanding the relationship between biodiversity and the capacity of ecosystems to perform multiple functions simultaneously (multifunctionality) has been a core ecological research topic in the last decade (1–4). In recent years, considerable research efforts have been devoted to explore how the biodiversity–ecosystem multifunctionality relationship (B–EMF relationship) is contingent upon the number and identity of ecosystem functions considered (e.g., refs. 5 and 6). In contrast, how multiple attributes of biodiversity such as the richness and abundance of species (taxonomic diversity) and the diversity of evolutionary lineages (phylogenetic diversity) and that of the traits related to resource use strategy (functional diversity) simultaneously influence ecosystem functioning remains poorly investigated (7–11), particularly at the global scale. Since these biodiversity attributes do not necessarily correlate (12, 13), assessing how they simultaneously influence multifunctionality is crucial not only to expand our fundamental understanding of the B–EMF relationships but also to prioritize relevant biodiversity attributes in global conservation programs and to improve management actions to preserve and restore terrestrial ecosystems (12, 14).

While most B–EMF studies have focused on species richness (1–3), functional diversity is also a key driver of multifunctionality (15–17). Higher functional diversity could enhance multifunctionality either because co-occurring species with contrasting trait values increase the overall resource utilization (18) or by including species that strongly affect ecosystem functioning (sampling effect; ref. 19). The phylogenetic diversity of plant communities can also influence ecosystem functions such as biomass production (7, 8). However, how phylogenetic diversity influences the B–EMF relationships remains unclear (20), and we do not know whether early diverging vs. recent evolutionary events ultimately influence ecosystem functioning (21). Phylogenetic diversity is a key biodiversity attribute when it effectively encompasses unmeasured biological traits that are relevant for ecosystem functioning (7, 22). As such, considering simultaneously phylogenetic diversity, which often grasps traits that are not typically measured [e.g., those related to plant–pathogen or plant–mycorrhiza interactions (23, 24)], and

## Significance

**Biodiversity is declining globally, but its different taxonomic, functional, and evolutionary attributes are doing so at a different pace. Understanding how these attributes influence ecosystem functioning is crucial to better predict the ecological consequences of biodiversity loss. Based on a survey of 123 drylands worldwide, our results highlight the phylogenetic and functional attributes of subordinate species as key drivers of the provision of multiple ecosystem functions simultaneously (multifunctionality). Our study expands our understanding of the relationship between biodiversity and multifunctionality by identifying the diversity of early diverging lineages and functional redundancy as important biodiversity attributes to prioritize in conservation and restoration programs aimed at promoting dryland multifunctionality worldwide.**

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measured traits could better account for the many dimensions of trait diversity exhibited by plant species (7, 13). Therefore, doing so could provide greater insights on how the multidimensionality of biodiversity influences multifunctionality.

No matter the taxonomic, phylogenetic, or functional attribute of biodiversity we look at, focusing solely on richness ignores the overwhelming effect that dominant species may have on ecosystem functioning (25, 26). According to the mass ratio hypothesis (25), the effect of plant species on ecosystem functioning is directly proportional to their biomass (mass ratio effects) and thus is relatively insensitive to the richness of subordinate species (25). This hypothesis was originally framed for individual functions related to biomass production and carbon cycling (25–27). However, the importance of the dominant species seems less clear when focusing on multifunctionality (28, 29) as it may depend on the attribute of biodiversity or the function considered.

To better understand the functional consequences of biodiversity changes occurring worldwide, we gathered data from 123 dryland ecosystems from six continents, including steppes, savannas, and shrublands (*SI Appendix, Fig. S1*), to investigate how multiple plant diversity attributes simultaneously influence multifunctionality. We used eight complementary biodiversity metrics that account for changes in the taxonomic, phylogenetic (early diverging and recent lineages), and functional diversity of plant communities (*Methods* and *SI Appendix, Fig. S2* and *Tables S1* and *S2*). Within this framework, our selection included metrics that were weighted and nonweighted by species abundance to disentangle the effect of dominant (mass ratio effects) vs. that of subordinate (richness effects) plant species on multifunctionality. After controlling for important climatic, soil, and geographic variables, we related multiple biodiversity metrics to four indices of multifunctionality using the multiple thresholds approach (30). The four indices were (i) multifunctionality (based on 11 weakly correlated functions), (ii) carbon cycling (C; including organic carbon concentration; pentose content and aboveground plant productivity), (iii) nitrogen cycling (N; including nitrate concentration, dissolved organic nitrogen, protein content, and potential nitrification), and (iv) phosphorus cycling (P; including available, inorganic and total phosphorus, and phosphatase enzymatic activity) (*SI Appendix, Table S3*). We tested the core hypothesis that considering multiple biodiversity attributes simultaneously increases the strength of biodiversity effects on multifunctionality.

## Results

The biodiversity metrics studied were strongly related to multifunctionality, even after accounting for the strong influence of geographic, climate, and soil properties on ecosystem functioning (Fig. 1). Biodiversity attributes explained up to 18% of multifunctionality (total variance) and up to 25, 22, and 27% of the variation in the indices derived for C, N, and P cycling, respectively. While species richness alone explained on average ~5% of variation in multifunctionality and up to 8% for C cycling, the inclusion of multiple biodiversity attributes enhanced the effect of biodiversity on multifunctionality by threefold. Functional, phylogenetic, and taxonomic biodiversity attributes were all selected in the most parsimonious models as significant predictors of multifunctionality, indicating that they have complementary effects on C, N, and P cycling.

Richness effects [the sum of explained variance of species richness and of nonweighted functional (FDIS) and phylogenetic (PSV and MNTD) metrics] explained between 76 and 100% of the biotic effects on multifunctionality (Fig. 2A). In contrast, the importance of dominant species through mass ratio effects (i.e., the metrics weighted by the abundance of the species) increased when considering each nutrient cycle individually (Fig. 2B–D). Mass ratio effects contributed, on average, to 51, 41, and 63% of the explained variance for C, N, and P cycling, respectively. Mass ratio effects were mostly related to the functional identity (CWM-SLA and CWM-H)

of dominant species rather than to their functional/phylogenetic diversities. In summary, richness effects due to subordinate species were the strongest predictors of multifunctionality, while mass ratio effects better explained C, N, and P cycling separately.

The net relationship between biodiversity and multifunctionality was generally positive, although weak, and even null when high multifunctionality thresholds were considered (Fig. 3A). This result was consistent regardless of the number of biodiversity attributes considered (Fig. 4) but varied with the nutrient studied. Thus, despite the larger amount of variance explained (Fig. 1), the net effect of biodiversity on ecosystem functioning was not stronger when multiple biodiversity attributes were included (Fig. 4). The inconsistency between variance explained and the net effect observed was mainly caused by contrasting effects of individual biodiversity attributes on different nutrient cycles taken separately and on overall multifunctionality.

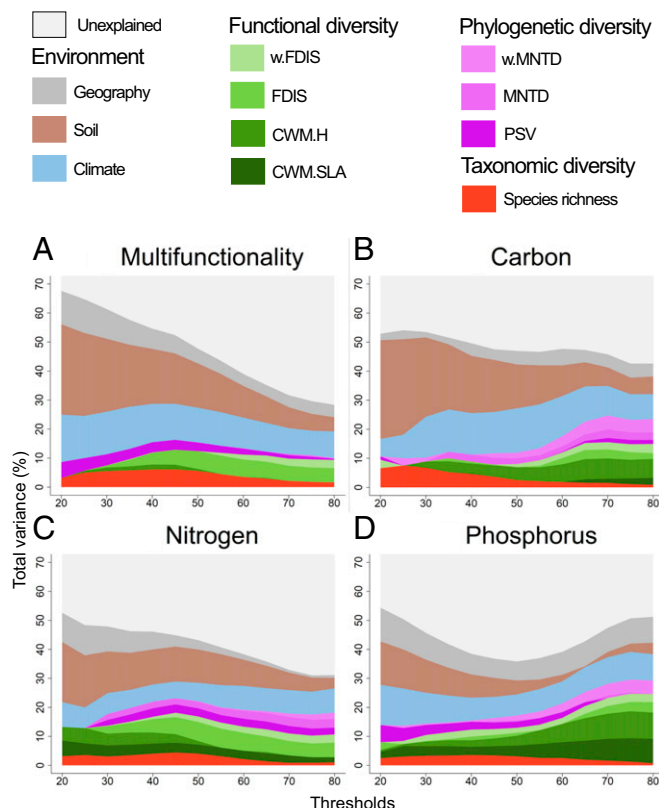
When evaluating the sets of functions separately, we observed positive relationships between biodiversity and C and P cycling (Fig. 3B and D), which turned negative in the case of N cycling (Fig. 3C). In addition, we observed contrasting relationships depending on the biodiversity attribute considered (Fig. 5). Species richness and phylogenetic diversity (PSV) were positively related to multifunctionality (Fig. 5A) and to C, N, and P cycling (Fig. 5B–D). However, FDIS (describing the dispersion of functional trait values observed within communities) was negatively related to multifunctionality, C, and N cycling. These results highlight that particular combinations of biodiversity attributes are needed to maximize either targeted nutrient cycles or overall multifunctionality.

## Discussion

We investigated how multiple biodiversity attributes (taxonomic, phylogenetic, and functional richness and mass ratio effects) simultaneously influenced the multifunctionality of 123 drylands worldwide. Together, these attributes explained up to 27% of variation in multifunctionality across a wide range of geographic contexts, climatic, and soil conditions. The simultaneous effect of multiple biodiversity attributes on multifunctionality stresses the need to move from a single taxonomic to a more multidimensional perspective of biodiversity to better grasp its complex effects on the functioning of terrestrial ecosystems. The importance of considering multiple biodiversity attributes has been recently shown for biomass production and its temporal variability, or for N availability (9–11, 31). Our results expand this research by highlighting how multiple biodiversity attributes differentially impact both multifunctionality and major nutrient cycles at the global scale.

Our study helps to reconcile two influential hypotheses on the effects of biodiversity on ecosystem functioning (19, 25). Mass ratio effects (i.e., the abundance-weighted metrics considered, accounting for the effect of the most dominant species) were the strongest predictors related to individual nutrient cycles but were weakly correlated with multifunctionality. As such, the mass ratio hypothesis may not apply when considering multiple functions simultaneously (see also ref. 28). In contrast, richness effects (those mainly driven by subordinate species) were the almost exclusive biotic drivers of multifunctionality in the drylands studied. Our results show that richness effects increase in importance when aiming at maximizing multiple ecosystem functions simultaneously. This matches the common view that species are unique, i.e., that a high number of cooccurring subordinate species can promote different functions at different times and places, therefore maximizing the performance of multiple functions simultaneously (1, 2, 5, 6). Our study extends the view of taxonomic diversity to the phylogenetic and functional attributes of subordinate species as important predictors of multifunctionality in terrestrial ecosystems.

Biodiversity had an overall positive effect on multifunctionality when considering multiple biodiversity attributes simultaneously. However, and contrary to our hypothesis, this effect was relatively



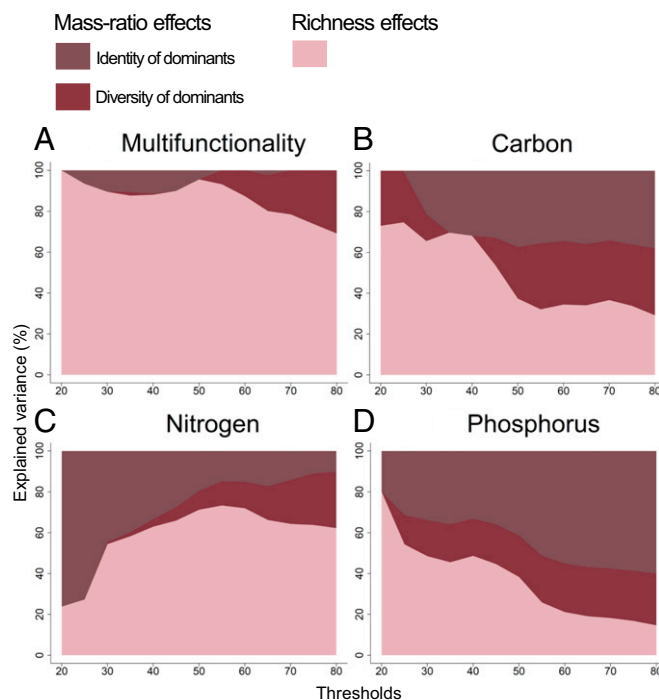
**Fig. 1.** Relative importance of eight uncorrelated biodiversity metrics, geographical, climatic, and soil predictors across multiple thresholds of (A) multifunctionality and (B–D) sets of functions related to C, N, and P cycling. The relative importance of predictors is expressed as the percentage of variance they explain and is based on the absolute value of their standardized regression coefficients. CWM.H and CWM.SLA, community-weighted mean for height and SLA; PSV, phylogenetic species variability; w.FDIS and FDIS, abundance-weighted and nonweighted functional dispersion; w.MNTD and MNTD, weighted and nonweighted mean nearest taxon distance.

weak (Figs. 3.4 and 4). The observed weak B–EMF relationship resulted first from contrasting relationships among the sets of functions relating to different biogeochemical cycles (Fig. 3 *B–D*). Also, we observed contrasting effects among the studied biodiversity attributes (Fig. 5). As a result, biodiversity effects on multifunctionality did not increase when considering multiple biodiversity attributes simultaneously (Fig. 4). These contrasting effects match with recent evidence reporting the occurrence of diverse (positive, neutral, and negative) biodiversity–ecosystem functioning relationships in real world ecosystems, especially when considering ecosystem functions other than plant biomass (4, 11, 32, 33). Our findings highlight that B–EMF relationships depend not only on the combination of functions studied (e.g., ref. 6) but also on the identity of biodiversity attributes considered. Therefore, ignoring the variety of attributes that biodiversity encompasses, such as taxonomic, phylogenetic, and functional diversity, or the influence of subordinate vs. dominant species may largely bias our ability to predict the consequences of biodiversity loss for the functioning of terrestrial ecosystems.

In opposition to the positive effect of species richness on multifunctionality and on C, N, and P cycling, functional richness (FDIS, the trait dispersion within communities) was negatively related to multifunctionality and C and N cycling (Fig. 5). This negative effect of FDIS is in line with previous observed negative effects of trait dispersion on dryland multifunctionality (17), as well as on the production and stability of biomass in several

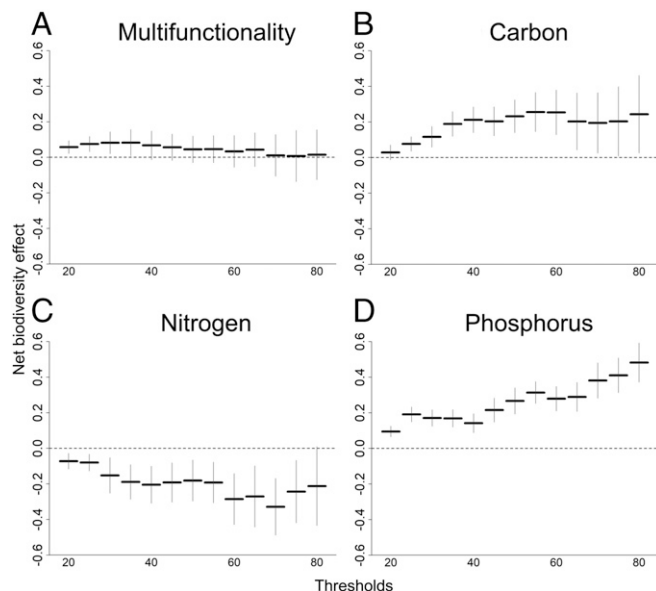
ecosystems (7, 10, 31). The contrasting effect between species richness and FDIS highlights the importance of functional redundancy within the studied communities to maintain high multifunctionality levels. This may be particularly true for communities experiencing strong abiotic stress such as dryland plant communities. Maximizing functional redundancy between species in drylands (31) may limit the inclusion of maladapted plant strategies particularly under drier conditions, which in turn may alter plant–soil feedbacks and accelerate land degradation and desertification processes (16, 17, 34).

Phylogenetic diversity played a significant role as driver of multifunctionality even after controlling for taxonomic and functional diversity, confirming the importance to consider this attribute in future B–EMF research. Phylogenetic diversity may reflect additional axes of functional specialization that are captured neither by maximum plant height nor by SLA, two fundamental traits reflecting plant resource use strategies (35). Phylogenetic diversity may effectively take into account hidden traits that are particularly relevant for the functioning of drylands [e.g., traits related to pathogen infection, pollination rates, or mycorrhizal associations (23) or to plant demographic strategies (36)] and thus are required to properly model B–EMF relationships. Dryland multifunctionality increased with a higher diversity of evolutionary lineages (PSV). The coexistence of species from both quaternary and tertiary periods are commonly observed in arid regions as a consequence of facilitative interactions (37). Also, PSV had opposite effects on multifunctionality compared with FDIS, indicating that maximizing both the phylogenetic distinctiveness and functional redundancy within species-rich communities are complementary drivers of higher ecosystem multifunctionality.



**Fig. 2.** Relative importance of mass ratio vs. richness effects across multiple thresholds of (A) multifunctionality and (B–D) sets of functions related to C, N, and P cycles. The importance of predictors is expressed as the percentage of variance they explain and is based on the absolute value of their standardized regression coefficients. Mass ratio effects were calculated as the sum of the variances explained by the abundance-weighted metrics (CWM.H, CWM.SLA, w.FDIS, and w.MNTD). Richness effects were calculated as the explained variances of nonweighted metrics (species richness, FDIS, PSV, and MNTD). Abbreviations are as in Fig. 1.



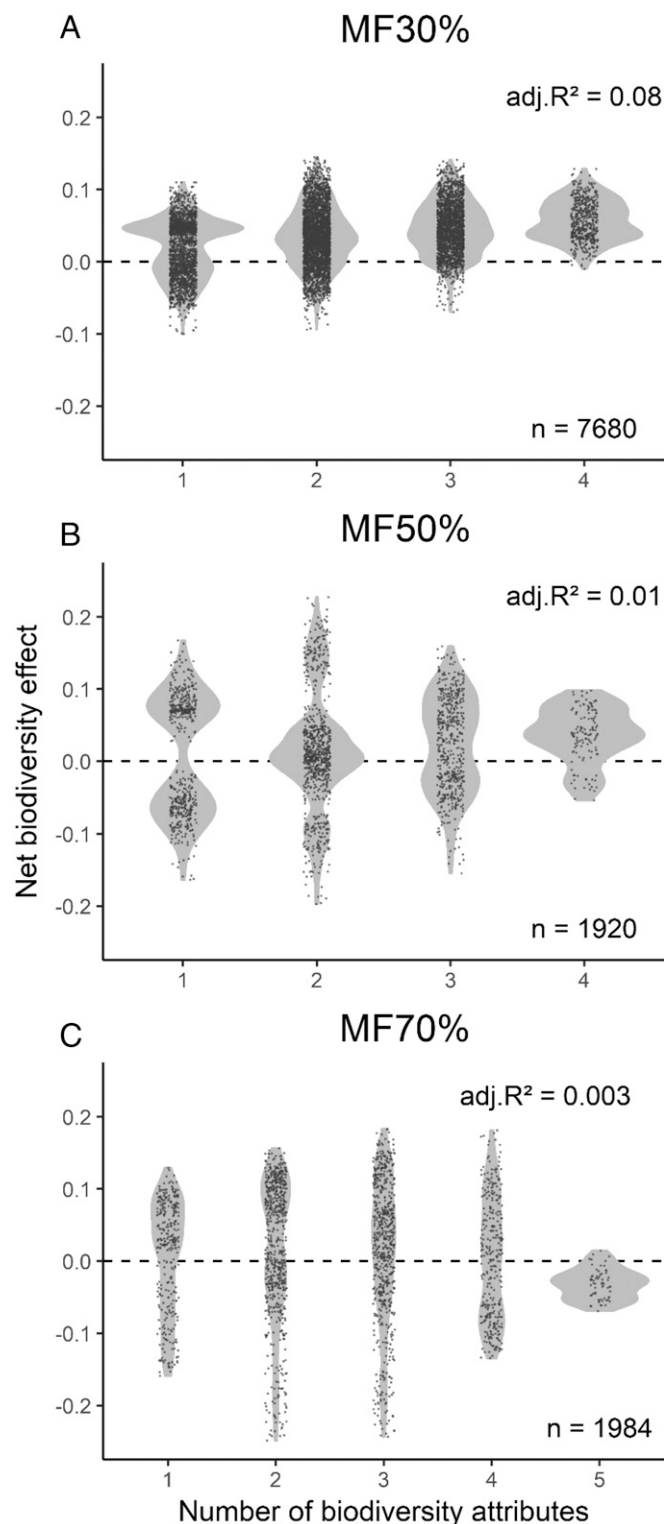


**Fig. 3.** Net effects of biodiversity attributes on (A) multifunctionality and on (B) carbon, (C) nitrogen, and (D) phosphorus cycling indices. The net effect was calculated as the sum of the standardized regression coefficients of all biodiversity metrics selected during the model selection procedures.

Our results also reflect that evolutionary distinct lineages shared similar maximum plant height and SLA attributes (see also ref. 38). This pattern may arise from both species filtering with suitable trait values and the adaptive evolution of traits in local lineages. A deeper understanding of the role of these processes could shed light on the importance of natural selection and convergent evolution as key evolutionary processes involved in the functioning of dryland ecosystems.

To further understand the linkages between the diversity of evolutionary lineages and multifunctionality, we investigated such relationships both at the most recent evolutionary events (tip level, MNTD) and across the whole tree (PSV). This approach revealed that both MNTD and PSV are related to ecosystem functioning in drylands worldwide (Figs. 1 and 5). While we observed exclusive effects of PSV on multifunctionality, those of MNTD were even stronger when considering individual nutrient cycles (positive and negative for C and N cycling, respectively). These B-EMF patterns indicate an increase in the importance of early diverging lineages with increasing the number of functions considered, i.e., that the diversity of more ancient lineages increases present-day multifunctionality. Alongside, recent evolutionary events might reflect recent innovations promoting C cycling and productivity (Fig. 5 and [SI Appendix, Tables S4 and S5](#)) without altering the level of multifunctionality. Our study was not designed to specifically investigate the changes in B-EMF relationships over evolutionary times. Nonetheless, the contrasted B-EMF patterns observed at two phylogenetic scales open new horizons on the importance of species evolutionary history for the emergence of multifunctional ecosystems, e.g., for tracking when biodiversity became an important multifunctionality driver.

Our results emphasize the need to consider the multidimensionality of biodiversity to better understand B–EMF relationships. The biodiversity attributes involved in individual nutrient cycles were mostly related to mass ratio effects. In contrast, richness effects enhanced multifunctionality through the diversity of early diverging lineages and functional redundancy within species-rich communities. In an era of global biodiversity crisis, our results can contribute to shape conservation, restoration, and management efforts based on species attributes to prioritize targeted nutrient



**Fig. 4.** Net effects of biodiversity on multifunctionality depending on the number of biodiversity attributes and multifunctionality thresholds considered. These effects are presented at (A) 30%, (B) 50%, and (C) 70% thresholds and are based on the number of plant diversity attributes retained in all models after the backward model selection procedure. The net effect was calculated as the sum of the standardized regression coefficients of all biodiversity attributes selected during the model selection procedures. Note that we used a violin function to highlight the density of points and a jitter function to visualize the data distribution.



the model. Then, a model selection procedure based on AICc selection ( $\Delta AICc < 2$ ) was applied on the resulting models to select the best predictors supported by the data. This procedure was performed using the  *dredge*  function in the R package  *MuMIn*  (49). Model residuals were inspected to ensure homoscedasticity and normality. All predictors and response variables were standardized before analyses using the Z-score to interpret parameter estimates on a comparable scale.

We evaluated the importance of the predictors under consideration as drivers of multifunctionality and sets of functions related to C, N, and P cycling. For doing so, we expressed the importance of predictors as the percentage of variance they explain, based on the comparison between the absolute values of their standardized regression coefficients and the sum of all standardized regression coefficients from all predictors in the models. This method is similar to a variance partition analysis because we previously transformed all predictors to Z-scores. The following identifiable variance fractions were then examined: (i) geography, (ii) climate, (iii) soil, and (iv) each of the different biodiversity metrics considered. We repeated this analysis to identify three variance fractions: the mass ratio effects through (i) the identity (CWM-H and CWM-SLA) and (ii) diversity of dominant species (w.FDIS and w.MNTD) and (iii) richness effects (all nonweighted metrics).

Net biodiversity effects were calculated as the sum of the standardized regression coefficients of all metrics of biodiversity selected during the model selection procedures. The data and supertree used in this paper are available in Figshare digital repository (50, 51).

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